

The Majority of Genetic Variation in Orangutan Personality and Subjective Well-Being is Nonadditive

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Abstract The heritability of human personality is well-established. Recent research indicates that nonadditive genetic effects, such as dominance and epistasis, play a large role in personality variation. One possible explanation for the latter finding is that there has been recent selection on human personality. To test this possibility, we estimated additive and nonadditive genetic variance in personality and subjective well-being of zoo-housed orangutans. More than half of the genetic variance in these traits could be attributed to nonadditive genetic effects, modeled as dominance. Subjective well-being had genetic overlap with personality, though less so than has been found in humans or chimpanzees. Since a large portion of nonadditive genetic variance in personality is not unique to humans, the nonadditivity of human personality is not sufficient evidence for recent selection of personality in humans. Nonadditive genetic variance may be a general feature of the genetic structure of personality in primates and other animals.

Keywords Heritability · Dominance genetic variance · Animal model · Nonhuman primate · Evolutionary psychology · Happiness

Introduction

Quantitative genetic studies of human personality traits such as those described by the Five-Factor Model (Digman 1990) show that the additive effects of genes influence personality variation and structure (Bouchard and Loehlin 2001). In addition, extended family designs found that nonadditive genetic effects account for over twice as much personality variance as additive genetic effects (Eaves et al. 1998; Keller et al. 2005; Pilia et al. 2006). Additive genetic variance comes from the independent effects of genes and is thereby eroded more efficiently by selection than nonadditive effects which arise from combinations of genes (Crnokrak and Roff 1995; Merilä and Sheldon 1999). High nonadditive genetic variance is therefore one sign of long-term directional or stabilizing selection. While the presence of nonadditive genetic effects on personality is consistent with balancing selection on personality (Penke et al. 2007) or with joint directional selection for personality and life-history traits (Figueredo and Rushton 2009), the ratio of additive to non-additive genetic variance alone is not a strong test of particular evolutionary mechanisms (Keller 2007).

A complementary approach to understanding a trait's evolutionary history is to see whether it exists in closely related species. This is because the most parsimonious explanation for species similarity is that the trait is ancestral, i.e., existed in a common ancestor, while the most parsimonious explanation for species differences is that they are the product of evolutionary divergence (Gosling and Graybeal 2007). Studies of nonhuman primate personality

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reveal dimensions akin to some or all of the Five-Factor Model domains and one or two dimensions not typically identified in humans, the most prominent being labeled “Dominance” or “Confidence”, which describe individual differences in competitive prowess (Freeman and Gosling 2010).

Chimpanzees are one of humans’ closest living relatives, sharing a common ancestor as recently as 4 million years ago (Hobolth et al. 2007) and, like humans, are highly gregarious (Goodall 1986). Given these facts, it should not be surprising that, alongside a Dominance dimension, chimpanzees possess five personality dimensions resembling the human Five-Factor Model (King and Figueredo 1997). One study found that chimpanzee Dominance is substantially heritable in the narrow-sense (Weiss et al. 2000), suggesting that genetic influences may underlie the personalities of chimpanzees and possibly other great apes.

Humans and chimpanzees shared a more distant ancestor approximately 15 million years ago (Purvis 1995) with orangutans, a semi-solitary great ape species (Galdikas 1985). Orangutans’ greater evolutionary distance from humans and chimpanzees and their lower levels of sociality would lead one to expect behavioral differences that are manifested in their personalities. This is, in fact, what is found. Orangutans possess five personality dimensions: three (Extraversion, Neuroticism, and Agreeableness) resemble like-named dimensions in humans and chimpanzees; one (Dominance) is a narrower version of its chimpanzee namesake; and one (Intellect) which resembles a combination of high Openness and high Conscientiousness, is a species-specific dimension (Weiss et al. 2006).

Another trait whose evolutionary history can be examined via cross-species comparisons is happiness or subjective well-being. In humans, subjective well-being refers to long-term pleasant and unpleasant affect as well as global satisfaction with one’s life (Diener et al. 1999). Far from being the consequences of one’s fortunes, subjective well-being is prospectively related to positive outcomes (Diener and Chan 2011; Lyubomirsky et al. 2005) and, like personality, is influenced by additive and nonadditive genetic variation (Bartels and Boomsma 2009; Caprara et al. 2009; Lykken and Tellegen 1996; Nes et al. 2006, 2010). One possible explanation for this is that subjective well-being is closely tied to personality; people lower in Neuroticism, higher in Extraversion, and higher in Agreeableness are generally happier (DeNeve and Cooper 1998). Moreover, these relationships appear to reflect genetic overlap as subjective well-being has a negative genetic correlation with Neuroticism and a positive genetic correlation with Extraversion, Conscientiousness, and Agreeableness (Weiss et al. 2008).

Chimpanzees (King and Landau 2003; Weiss et al. 2009) and orangutans (Weiss et al. 2006) also display

individual differences in subjective well-being. As chimpanzee and orangutan subjective well-being is assessed by observers, it is not “subjective” in the human sense, i.e., individuals’ reports of their own happiness and life satisfaction (Diener et al. 1999). However, the term is appropriate since the ratings capture normal variation in overall mood or affect as opposed to physical health or well-being that is not an individual difference, such as through environmental enrichment applied to an entire captive enclosure (King and Landau 2003; Weiss et al. 2006).

Beyond the face validity of the subjective well-being scale used in these studies, there is evidence that observer ratings of chimpanzee and orangutan subjective well-being tap the same underlying construct as human self-reports. For example, lower Neuroticism, higher Extraversion, and higher Agreeableness translate into higher chimpanzee and orangutan subjective well-being (King and Landau 2003; Weiss et al. 2006, 2009), a result similar to that in humans (DeNeve and Cooper 1998; Steel et al. 2008). In addition, orangutan subjective well-being is prospectively related to longevity (Weiss et al. 2011a). Finally, approximately 40 % of chimpanzee subjective well-being variance is heritable in the narrow-sense and these additive genetic effects overlap with those that contribute to individual differences in Dominance (Weiss et al. 2002).

Studying chimpanzees and humans alone does not allow one to determine how much of the common genetic components of the relationship between personality and subjective well-being are shared with a common ancestor. This is because the existing findings do not rule out the possibility that the genetic nexus underlying the personality-subjective well-being correlations arose independently in these species as, for example, an adaptation to social environments where encounters with other individuals are frequent. As a semi-solitary species closely related to humans and chimpanzees, the presence or absence of a similar genetic structure between personality and subjective well-being in orangutans can be used as evidence to differentiate between those features that are ancestral and those that are derived. Therefore, for the present study, we will explore the quantitative genetic structure of personality and subjective well-being in orangutans that have been rated on reliable and well-validated personality and subjective well-being questionnaires (Weiss et al. 2006). We relied on these questionnaires because they allowed us to obtain the large sample size required for accurate heritability estimates. The present study will enable us to determine whether nonadditive genetic variance underlies personality and subjective well-being variance in another primate species and whether the genetic basis of subjective well-being is a unique feature of chimpanzees and humans. If a large proportion of the genetic variance in orangutan personality can be attributed to nonadditive effects, it

would support the idea that similar evolutionary processes maintain variation in personality across primate species. Alternatively, if nonadditive effects are absent or small in orangutans relative to additive genetic variance, then this would make selection or other evolutionary processes unique to the hominid lineage a more likely explanation for the genetic structure of human personality.

Method

Participants and pedigree

Subjects were 54 Bornean (*Pongo pygmaeus*), 100 Sumatran (*Pongo abelii*), and 30 hybrid orangutans housed across 42 zoological parks in the United States, Canada, Australia, and Singapore. Each zoo held between 1 and 22 orangutans (mean = 4.3, mode = 3). There were 109 females and 75 males (mean age = 21.6, SD = 12.1). Of these orangutans, 152 participated in a previous study of personality (Weiss et al. 2006) while ratings on the additional 32 orangutans, from zoos in Australia and Singapore, were new to this study.

The orangutans were connected across zoos through an extended pedigree containing 358 individuals and encompassing up to four generations. Both the mother and father were known for 158 of the subjects. Only the mother was known for 27 subjects and only the father for one subject. Among the genetically informative individuals contributing to estimates of quantitative genetic parameters there were 50 full sibships and 134 half sibships. The pedigree also contained two inbred individuals.

Personality and subjective well-being

Orangutan personality consists of five dimensions: Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect (Weiss et al. 2006) defined by the intercorrelations among items describing orangutan personality. Extraversion captures differences in interpersonal traits and is defined by items such as *playful*, not *solitary*, and *social* but differs from human and chimpanzee Extraversion by also including aspects of Openness, such as *inquisitive*. Dominance, as in chimpanzees, is defined by traits related to dominance and submissive behaviours and traits similar to the negative pole of human Agreeableness, such as *manipulative* and *aggressive*. Neuroticism is made up of traits similar to human Neuroticism such as *anxious*, not *stable*, and *impulsive*. Agreeableness was similar to the identically named dimension in chimpanzees and is defined by items related only to the positive pole of human Agreeableness, such as *sympathetic* and *protective*. Finally, Intellect was made up of items similar to both human

Conscientiousness (*decisive*, not *disorganized*) and Openness (*intelligent*).

Personality was measured by ratings of each individual provided by 113 zoo employees who worked regularly with the orangutans and who did not receive training on measuring personality. Each orangutan was rated by between 1 and 7 raters (mean = 2.6). Personality ratings were made on one of three versions of the same questionnaire: 137 subjects were rated on the 48-item Orangutan Personality Questionnaire (OPQ, Weiss et al. 2006), 37 subjects were rated on the expanded 54-item Hominoid Personality Questionnaire (HPQ, Weiss et al. 2009), and 10 subjects were rated on an earlier, 43-item version of the OPQ that was based on the Chimpanzee Personality Questionnaire (King and Figueredo 1997). Each item on these questionnaires consisted of an adjectival descriptor and one to three sentences clarifying the adjective in term of orangutan behavior. For example, *active* was defined as “Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.” Ratings were made on a 7 point scale. Across all raters and subjects the data contained 20,446 personality item scores.

Subjective well-being was assessed in 164 orangutans by ratings on four items: their balance of positive and negative moods, the degree to which they enjoyed social interactions, their ability to achieve goals, and by asking raters to indicate how happy they would be if they were the target orangutan for a week. The items were identical to those used to assess chimpanzee subjective well-being in prior studies (King and Landau 2003; Weiss et al. 2009). In total there were 1,578 subjective well-being item scores included in the analysis.¹

Assessing personality in nonhuman primates using ratings such as these sometimes arouses skepticism (Uher 2008a, b). However, multiple studies in great apes and Old World monkeys support the reliability and validity of such ratings (see review by Freeman and Gosling 2010). For instance, there is moderate to high agreement among raters (King and Figueredo 1997; King and Landau 2003; Uher and Asendorpf 2008; Weiss et al. 2006) and ratings are stable over time (Capitanio 1999; King et al. 2008; Stevenson-Hinde et al. 1980; Uher and Asendorpf 2008; Weiss et al. 2011b). In addition, the personality structure derived from chimpanzee personality ratings replicated in three independent samples (King et al. 2005; Weiss et al. 2007, 2009). Finally, the pattern of correlations between ratings and specific behaviors supports the convergent and discriminant validity of ratings (Konečná et al. 2008;

¹ Both personality and subjective well-being questionnaires can be obtained from <http://www.sciencedirect.com/science/article/pii/S0006322311008572>.

Pederson et al. 2005; Uher and Asendorpf 2008). Ratings of subjective well-being in nonhuman primates also show high reliability (King and Landau 2003; Weiss et al. 2006, Weiss et al. 2011b) and shows external validity by, for example, its associated with outcomes such as mortality in orangutans (Weiss et al. 2011a).

Quantitative genetic analysis

Heritability estimates are based on correlations among the phenotypes of individuals who differ in their amount of genetic relatedness. Behavior genetic studies of humans typically use the difference in correlations between monozygotic and dizygotic twins as the basis for heritability estimates (Bouchard and Loehlin 2001). Because we had a pedigree and thus could calculate relatedness among all the individuals in the sample, we used an “animal model” to estimate heritability. The animal model is a biometrical genetic model increasingly used in human studies (Pilia et al. 2006) and is commonly used in agriculture and evolutionary genetics (Kruuk 2004; Lynch and Walsh 1998; Wilson et al. 2009).

Just as twin models can be viewed as a particular instance of a structural equation model, the animal model is a type of multilevel or mixed-effects model. If a trait is influenced by genetic differences, two genetically related individuals should deviate from the mean in the same direction and by a similar amount; both corresponding to how closely related these individuals are. For example, full siblings should be more similar in their deviation from the mean than full cousins. The additive genetic relationships among animals are used as the basis for a random effect estimating an individual’s deviation from the mean phenotype attributable to additive genetic effects (Kruuk 2004; Lynch and Walsh 1998). The proportion of variance attributable to these genetic deviations is an estimate of the trait’s heritability. Similarly, information about the extent to which individuals share genotypes (for example, full siblings will on average share half their genes but will have only a quarter of their genotypes in common) can be used to estimate nonadditive sources of genetic variance such as dominance genetic variance. While in most twin models dominance genetic variance is confounded with shared family effects, these can be separated using extended twin family designs (Eaves et al. 1978) or pedigree data containing a large number of full- and half-siblings (Wilson et al. 2009), as was the case with the orangutan pedigree. We also explored whether heritability estimates were consistent between the Bornean and Sumatran orangutans. Significant differences in genetic structure between these species could be a potential signal of evolutionary divergence in their personality or subjective well-being.

Individuals who share environments may also resemble each other in terms of their personality or subjective well-being. We therefore considered whether individuals with the same mother or who lived in the same zoo environment when rated were more similar than those living in different zoo environments. The maternal environment captures effects that make offspring of the same mother resemble each other (independent of transmitted genes) such as natal effects or rearing style and may be caused by either environmental effects or indirect genetic effects. A zoo environment effect would account for any features of the captive environment that make individuals living together more similar to each other. We explored the amount of variance in each personality trait and subjective well-being that these effects accounted for by fitting a series of univariate models. We then estimated genetic and environmental covariances among traits using a multivariate model.

Measurement component

Rather than analyzing factor scores for each personality trait, we built the models up from each rater’s assessments of each orangutan on every item and thus modeled personality and subjective well-being as latent variables. Each rating on the 7-point scale was treated as ordinal and connected to an underlying latent scale with a probit link parameterized using cut-points (Hadfield and Nakagawa 2010). Each item contributed to the latent score of the personality domain it had a salient loading on as described previously (Weiss et al. 2006). We reverse coded items with negative loadings. This approach handled heterogeneity in the number of items for each personality domain that was a consequence of the different versions of the questionnaires used to rate the orangutans. Using the raw observations allowed uncertainty about individual orangutans’ personality scores to propagate through the model and thus allowed us to control for relationships among personality and subjective well-being domains introduced by raters. All models used residual variances fixed to 1 while residual covariances in the multivariate model were fixed to 0 because each item only gave information on one personality or subjective well-being domain.

Variance partition component

One advantage of using the animal model for heritability estimates is that it can be extended to include fixed effects that are known to affect the phenotype as well as additional group-level random effects to partition the variance (Kruuk 2004). In all models we controlled for potential differences attributable to age and sex by fitting them as fixed effects. We started with models that estimated individual orangutan

(V_{ID}) and rater (V_J) variances (model 1) using orangutan and rater IDs as predictors. We then added parameters to estimate additive genetic variance (V_A) for all species together (model 2) using a design matrix derived from the additive genetic relationship matrix calculated from the pedigree. We created models that estimated nonadditive genetic variance (V_D , model 3) using the dominance genetic relationship matrix (Lynch and Walsh 1998, p. 768).

We then created models that fit random effects using the mother and zoo IDs to estimate maternal environment variance (V_M , model 4) and shared zoo environment variance (V_Z , model 5). We also fit a model that included all the effects (model 6) to give more conservative estimates of effects that are difficult to separate when families share a common environment (Wilson et al. 2009). In the models that estimate additive and nonadditive genetic or maternal and zoo environment variances, the orangutan identity matrix fits an effect comparable to the unique environment variance (V_E) in twin models, that is, effects that cause an orangutan to differ from other individuals who share genes or environments. We additionally tested models that fit unique environment effects separately for each species group (Bornean, Sumatran, and hybrid) and additive and dominance genetic effects for Bornean and Sumatran orangutans (model 7). We did this by creating separate genetic relationship matrices for each species.

Model fitting

We estimated fixed effects and components of variance using a Bayesian animal model (Sorensen and Gianola 2002) as implemented in MCMCglmm (Hadfield 2010). We used Bayesian methods because they better handle confounded variables (Ovaskainen et al. 2008) such as parents and offspring who shared genes and a zoo environment. Bayesian inferences can be made by summarizing random draws from the joint posterior distribution of the parameter estimates. MCMCglmm uses an inverse-Wishart distribution as the prior for variance components. We specified priors with variances of 1 and covariances of 0 and degrees of freedom parameter of 1 for the univariate models and 6 for the multivariate models. We ran the models for 10^6 iterations, discarded the first half of the samples, and thinned the samples from the posterior distribution to 1,000. The autocorrelations among the successive samples from the posterior distributions were less than .1. We compared model fit using the deviance information criterion or DIC (Hadfield 2010). Because there is error in calculating DIC from the Monte Carlo simulations, we ran each model twice.

Model inference

To exclude measurement error from our heritability estimates, we calculated heritability as the ratio between the additive genetic variance and the repeatable variance ($V_{RPT} = V_A + V_D + V_M + V_Z$) on the latent variable scale as $h^2 = V_A/V_{RPT}$. The heritability estimate thus only reflects variance from effects assigned to individual orangutans and not measurement variance from rater effects and the probit distribution used to model item scores. We calculated the broad-sense heritability as $H^2 = (V_A + V_D)/V_{RPT}$ and the proportion of nonadditive genetic variance (Crnokrak and Roff 1995) as $D_x = V_D/(V_A + V_D)$. We estimated correlations among traits attributable to additive genetic (r_A), nonadditive genetic (r_D), and unique environment (r_E) effects as well as rater effects (r_J) using a multivariate animal model. Covariances, like variances, can also be added together, so we also examined the total genetic correlations (r_G) from adding the additive and nonadditive genetic covariance matrices ($\text{cov}_G = \text{cov}_A + \text{cov}_D$) and the phenotypic correlations among personality and subjective well-being statistically controlling for rater effects ($\text{cov}_P = \text{cov}_A + \text{cov}_D + \text{cov}_E$).

Because studies of humans and chimpanzees found that all or most of the genetic variance underlying subjective well-being was shared with personality, we calculated the conditional genetic variance of subjective well-being. The conditional genetic variance is genetic variance that is unique to subjective well-being, excluding variance from genetic factors that also influence the personality domains (Hansen and Houle 2008), defined as

$$c(y|\mathbf{x}) = G_y - \mathbf{G}_{yx}\mathbf{G}_x^{-1}\mathbf{G}_{xy}$$

where $\mathbf{G}_{yx}$ and $\mathbf{G}_{xy}$ are vectors of the genetic covariance between y and the other traits and $\mathbf{G}_x$ is the genetic covariance matrix of the other traits.

Reliability analysis

We calculated the reliabilities of the personality and subjective well-being assessments as intraclass correlation coefficients (ICCs) in two ways using estimates from the genetic models. First, to estimate the consistency of the items making up each personality domain or subjective well-being, we calculated the ratio of the animal variance (that is, the repeatable variance from genetic or environmental effects that are assigned to individual animals) plus the rater variance over the residual and link function variances ($V_{RPT} + V_J$)/($V_{RPT} + V_J + V_R + 1$) where the final 1 is from the variance of the probit distribution used to model the ordered categorical scores. This ICC is on the scale of the raw data and represents the expected correlation between an individual's scores on two items made by

the same rater. Although it is not the same as Cronbach's α , it specifies the degree to which the rating of an individual on one item generalized to other items on that scale and is therefore a type of model-derived estimate of internal consistency. Second, we calculated reliability on the latent scale as $V_{\text{RPT}}/(V_{\text{RPT}} + V_j)$ to represent the expected correlation between two assessments of the same individual by different raters. This ICC estimates interrater agreement and is similar to ICC(3,1) (Shrout and Fleiss 1979).

Results

Genetics

We built a series of models to estimate the variance in personality and subjective well-being attributable to the additive and nonadditive (dominance) effects of genes, the maternal environment, and the zoo environment that conditioned on effects from raters. Because of the variance in the DIC between the two runs of each of the univariate models (Table 1), it was not possible to definitively choose the best model for each personality domain. We therefore interpreted the modes and credible intervals for each parameter estimate for all models.

Variance components, heritability, and the other variance proportion coefficients of models 1–6 are given in Tables 1 and 2. The narrow-sense heritabilities of personality traits and subjective well-being in orangutans were moderate and across the models and traits ranged from about 20–30 % of the repeatable variance (Table 2; Fig. 1). The nonadditive genetic effects explained on average more of the variance (30–50 %) than additive genetic effects. The total genetic effects (broad-sense heritability or H^2) thus accounted for upwards of three quarters of the repeatable variance (Table 3; Fig. 1). The proportion of nonadditive genetic variance (D_x) was greater than half for all traits (Table 2). The estimates for maternal environment and zoo effects were low but the variance accounted for by nonadditive genetic effects was generally reduced when a maternal environment effect was included in the model. The separate heritability estimates for Bornean and Sumatran orangutans (Table 3) were consistent with the estimates from the whole sample.

While there was uncertainty in the additive genetic (r_A), nonadditive genetic (r_D), and unique environment (r_E) correlations between personality and subjective well-being (Table 4), the effects all went in the same direction (negative for Neuroticism and positive for Extraversion, Dominance, Agreeableness, and Intellect). Using the conditional genetic variances, we determined that 15 % (95% credible interval [CI] = .03, .38) of the additive genetic and 19 % (95% CI = .05, .44) of the nonadditive genetic

variance in subjective well-being was shared with personality. From these models we were also able to derive estimates of the phenotypic correlations among personality and subjective well-being that controlled for covariances among traits attributable to rater effects which were Extraversion $r_P = .24$ (95% CI = .05, .37), Dominance .13 (95% CI = -.09, .28), Neuroticism $-.22$ (95% CI = $-.38, -.05$), Agreeableness .20 (95% CI = .05, .40), and Intellect .18 (95% CI = .02, .36). There was also some evidence for a positive dominance genetic and unique environment correlation between Agreeableness and Extraversion (Table 4).

Psychometrics

Using the fitted genetic models we estimated the reliability of the orangutan personality ratings. The intraclass correlation coefficient from the animal and rater variances on the scale of the raw data, which represents the expected correlation between two items assessed on the same animal by the same rater and can act as a form internal consistency of items making up each scale, ranged from .21 for Intellect to .41 for Agreeableness and was .49 for subjective well-being (Table 5). Combining information from multiple raters produced highly reliable assessments of latent personality values which ranged from .73 for Intellect to .87 for Dominance. Reliability of subjective well-being on the latent scale was .60, and thus acceptable.

Rater effects contributed to the observed correlations among personality and subjective well-being scores (Table 4). After decomposing the covariance among personality and subjective well-being into animal components (genetic and environment) and a rater component, raters who rated an orangutan as higher on Extraversion, Dominance, Agreeableness, and Intellect and lower on Neuroticism also tended to rate that orangutan as higher on subjective well-being. Notably, the estimate of rater effects for the correlation between Dominance and subjective well-being correlation tended to go in the opposite direction from genetic and unique environmental estimates. There were also detectable rater effects on the Extraversion–Agreeableness, Extraversion–Intellect, Neuroticism–Intellect, and Agreeableness–Intellect correlations.

Discussion

We found that the most genetic variation in orangutan personality and subjective well-being could be assigned to nonadditive genetic effects. This is consistent with the results from human personality research (Eaves et al. 1998; Keller et al. 2005; Pilia et al. 2006). The narrow-sense heritability estimates of about 20 % were likewise

Table 1 Variance components and model fit criteria

Model	DIC	V_E (V_{ID})	V_A	V_D	V_M	V_Z	V_I
Extraversion							
1	16,046; 16,046	.53 (.41, .68)					.14 (.10, .24)
2	16,036; 16,046	.38 (.25, .55)	.17 (.06, .32)				.17 (.10, .23)
3	16,028; 16,036	.18 (.09, .38)	.15 (.07, .29)	.22 (.10, .40)			.14 (.10, .24)
4	16,031; 16,002	.33 (.22, .53)	.16 (.07, .32)		.09 (.06, .20)		.14 (.10, .23)
5	16,042; 16,026	.36 (.24, .57)	.13 (.08, .36)			.11 (.06, .24)	.13 (.10, .24)
6	15,978; 16,018	.20 (.07, .36)	.14 (.06, .30)	.17 (.08, .35)	.09 (.06, .22)	.11 (.06, .26)	.15 (.09, .23)
Dominance							
1	17,788; 17,792	1.0 (.77, 1.2)					.17 (.10, .25)
2	17,781; 17,790	.82 (.47, 1.0)	.25 (.09, .57)				.16 (.10, .25)
3	17,778; 17,787	.21 (.08, .60)	.18 (.07, .44)	.58 (.24, .92)			.16 (.11, .26)
4	17,791; 17,785	.57 (.34, .88)	.19 (.08, .51)		.21 (.08, .46)		.18 (.11, .25)
5	17,779; 17,781	.84 (.5, 1.05)	.24 (.09, .56)			.11 (.05, .27)	.16 (.11, .25)
6	17,777; 17,776	.27 (.10, .61)	.18 (.07, .45)	.22 (.12, .66)	.18 (.07, .45)	.13 (.06, .29)	.16 (.11, .26)
Neuroticism							
1	13,543; 13,540	.42 (.32, .55)					.11 (.07, .19)
2	13,524; 13,536	.33 (.20, .45)	.14 (.06, .25)				.11 (.07, .18)
3	13,532; 13,535	.14 (.07, .29)	.10 (.06, .23)	.20 (.10, .36)			.10 (.07, .18)
4	13,524; 13,523	.29 (.16, .41)	.12 (.06, .25)		.13 (.06, .23)		.12 (.07, .18)
5	13,531; 13,529	.31 (.2, .43)	.12 (.06, .25)			.15 (.05, .28)	.11 (.07, .17)
6	13,524; 13,510	.14 (.08, .26)	.10 (.05, .21)	.13 (.07, .27)	.10 (.06, .22)	.13 (.06, .30)	.11 (.07, .17)
Agreeableness							
1	10,129; 10,098	.95 (.72, 1.2)					.36 (.24, .55)
2	10,134; 10,088	.73 (.47, 1.1)	.19 (.09, .49)				.40 (.25, .56)
3	10,124; 10,126	.23 (.08, .65)	.15 (.08, .40)	.56 (.23, .87)			.38 (.24, .57)
4	10,123; 10,125	.67 (.37, .95)	.16 (.08, .49)		.19 (.08, .40)		.38 (.24, .58)
5	10,091; 10,115	.70 (.46, 1.0)	.20 (.08, .51)			.15 (.08, .46)	.34 (.23, .52)
6	10,122; 10,121	.26 (.13, .68)	.19 (.09, .42)	.36 (.09, .65)	.17 (.07, .36)	.18 (.06, .44)	.34 (.24, .54)
Intellect							
1	8,149; 8,149	.48 (.35, .64)					.24 (.15, .37)
2	8,149; 8,149	.31 (.17, .49)	.21 (.09, .39)				.28 (.15, .37)
3	8,087; 8,136	.15 (.08, .35)	.19 (.07, .33)	.23 (.09, .38)			.21 (.15, .35)
4	8,144; 8,148	.29 (.13, .45)	.18 (.08, .42)		.12 (.05, .23)		.27 (.13, .37)
5	8,131; 8,123	.33 (.16, .48)	.23 (.07, .39)			.15 (.06, .34)	.18 (.13, .34)
6	8,144; 8,143	.17 (.08, .33)	.16 (.06, .32)	.14 (.06, .30)	.12 (.05, .23)	.14 (.07, .33)	.22 (.13, .35)
Subjective well-being							
1	4,222; 4,195	.92 (.65, 1.3)					.69 (.43, .96)
2	4,174; 4,234	.64 (.31, 1.0)	.29 (.08, .76)				.65 (.43, .98)
3	4,212; 4,234	.21 (.09, .68)	.19 (.07, .53)	.49 (.17, .90)			.62 (.44, 1.0)
4	4,230; 4,247	.56 (.17, .83)	.28 (.08, .63)		.19 (.08, .55)		.67 (.44, 1.0)
5	4,249; 4,228	.72 (.31, 1.1)	.21 (.07, .69)			.20 (.06, .58)	.53 (.40, .95)
6	4,242; 4,217	.32 (.10, .58)	.23 (.06, .50)	.20 (.10, .62)	.23 (.07, .50)	.25 (.09, .57)	.67 (.43, 1.0)

DIC Deviance information criterion, with values from two runs of each model. Model for each personality dimension with the lowest average DIC is highlighted in bold although the variance in DIC meant it was not possible to choose overall best models based on parsimony criteria. V_E unique environment variance, V_I individual variance, V_A additive genetic variance, V_D nonadditive (dominance) genetic variance, V_M maternal environment variance, V_Z zoo environment variance, V_J rater variance. V_R Residual variance, fixed at 1 in all models. The first variance component column gives V_{ID} for model 1 and V_E for all other models. Posterior modes of each estimate are given with 95% credible intervals in parentheses

Table 2 Variance partition coefficients

Model	$h^2 = V_A/V_{RPT}$	$d^2 = V_D/V_{RPT}$	$m^2 = V_M/V_{RPT}$	$z^2 = V_Z/V_{RPT}$	$e^2 = V_E/V_{RPT}$	$D_x = V_D/(V_A + V_D)$
Extraversion						
2	.30 (.13, .53)				.70 (.47, .87)	
3	.23 (.13, .45)	.32 (.17, .55)			.38 (.18, .60)	.63 (.34, .80)
4	.25 (.11, .46)		.19 (.09, .29)		.51 (.37, .75)	
5	.22 (.11, .46)			.17 (.08, .30)	.54 (.34, .73)	
6	.16 (.08, .33)	.20 (.09, .40)	.13 (.07, .24)	.13 (.07, .28)	.29 (.09, .41)	.51 (.28, .77)
Dominance						
2	.21 (.07, .49)				.79 (.51, .93)	
3	.22 (.08, .42)	.35 (.18, .70)			.27 (.11, .60)	.73 (.45, .91)
4	.19 (.07, .42)		.17 (.09, .38)		.60 (.31, .74)	
5	.18 (.08, .44)			.09 (.05, .22)	.71 (.43, .82)	
6	.15 (.06, .32)	.21 (.09, .48)	.20 (.06, .33)	.09 (.04, .20)	.19 (.08, .45)	.73 (.34, .87)
Neuroticism						
2	.30 (.13, .50)				.70 (.50, .87)	
3	.22 (.12, .42)	.36 (.19, .58)			.38 (.15, .55)	.69 (.43, .83)
4	.21 (.11, .42)		.24 (.11, .39)		.49 (.29, .66)	
5	.23 (.11, .40)			.25 (.12, .41)	.48 (.34, .68)	
6	.15 (.07, .)	.17 (.10, .)	.16 (.09, .)	.18 (.10, .)	.24 (.10, .)	.57 (.34, .77)
Agreeableness						
2	.18 (.08, .43)				.82 (.57, .92)	
3	.22 (.06, .38)	.52 (.17, .69)			.24 (.12, .60)	.78 (.45, .89)
4	.14 (.08, .41)		.14 (.07, .33)		.64 (.38, .8)	
5	.19 (.07, .40)			.20 (.07, .31)	.61 (.36, .77)	
6	.14 (.06, .30)	.19 (.07, .46)	.13 (.05, .24)	.15 (.06, .29)	.27 (.09, .47)	.61 (.30, .83)
Intellect						
2	.35 (.21, .68)				.65 (.32, .79)	
3	.29 (.14, .52)	.28 (.14, .53)			.29 (.13, .55)	.52 (.27, .78)
4	.28 (.13, .57)		.20 (.09, .33)		.43 (.21, .65)	
5	.23 (.14, .53)			.22 (.10, .40)	.41 (.21, .64)	
6	.16 (.08, .35)	.15 (.08, .34)	.14 (.06, .25)	.21 (.09, .35)	.18 (.09, .38)	.51 (.23, .72)
Subjective well-being						
2	.18 (.09, .64)				.82 (.36, .91)	
3	.24 (.07, .47)	.38 (.15, .65)			.24 (.11, .60)	.78 (.37, .89)
4	.19 (.08, .51)		.26 (.08, .47)		.47 (.20, .72)	
5	.18 (.05, .52)			.16 (.07, .38)	.54 (.25, .77)	
6	.15 (.04, .33)	.21 (.05, .39)	.19 (.06, .34)	.14 (.07, .34)	.17 (.07, .40)	.55 (.25, .84)

Heritability (h^2) and variance partition coefficients for nonadditive (dominance) genetic (d^2) and maternal (m^2), zoo (z^2) and unique (e^2) environments calculated relative to the repeatable variance, $V_{RPT} = V_A + V_D + V_M + V_Z + V_E$. D_x = proportion of nonadditive genetic variance

consistent with human findings that used a similarly specified, pedigree-based animal model (Pilia et al. 2006). This suggests that a high proportion of nonadditive genetic variance may be a common feature of personality in primates under long-term directional or stabilizing selection and not exclusively the result of evolutionary processes unique to the human lineage. Our low estimates of shared zoo environment effects on personality match results from chimpanzees (Weiss et al. 2000) and are consistent with

findings from human personality research on the effect of the shared (family) environment (Bouchard and Loehlin 2001).

While we lacked enough power to get precise estimates of genetic correlations between personality and subjective well-being, the direction of the correlations matched results from chimpanzees (Weiss et al. 2002) and humans (Weiss et al. 2008). Human and great ape subjective well-being may therefore have a common genetic basis in personality

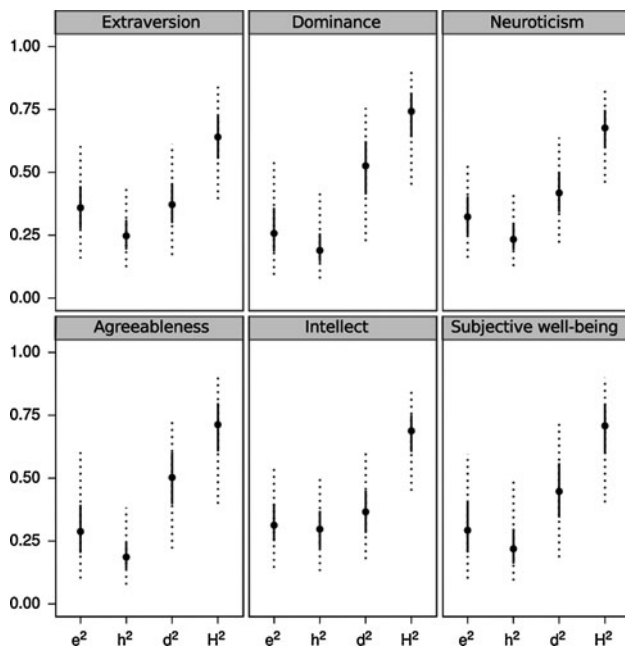


Fig. 1 Variance proportion coefficients for repeatable variance. Points indicate posterior modes of each estimate with 50 % credible intervals in *solid* and 95% credible intervals in *dotted lines*. h^2 = (narrow-sense) heritability, d^2 = dominance, H^2 = broad-sense heritability, e^2 = unique environment. Figure by the authors, licensed under a Creative Commons Attribution Unported License and published under the terms of this license

traits related to emotional stability and social assertiveness. However, unlike chimpanzees and humans, less than half of the genetic variance in orangutan subjective well-being could be explained by genetic effects shared with personality. Thus, while the personality–subjective well-being link is likely ancestral in great apes, the greater genetic overlap in humans and chimpanzees may be a derived characteristic. Alternatively, personality and subjective well-being may have become more genetically uncoupled as orangutans diverged from these species.

In our models we used the dominance genetic relationship matrix, defined as the probability that two individuals

share the same genotype at a locus (Lynch and Walsh 1998), to estimate nonadditive genetic variance. Dominance genetic variance comes from interactions between alleles at the same locus but additive $\times$ additive and other epistatic interactions could also contribute to nonadditive genetic variance. However, as only small fractions of variance from epistatic effects contributes to correlations among related individuals, the design matrix needed to estimate them will be very close to that used to estimate dominance genetic relationships. Therefore our estimate of nonadditive genetic variance would include some variance from any epistatic effects.

Our results also show the importance of conditioning on rater effects and other sources of measurement error when analyzing questionnaire-based assessments of animal personality. To wit, while raters were consistent in the scores they assigned to individual subjective well-being items, the interrater reliability of subjective well-being was lower than for the personality traits, which is consistent with the subjective well-being factor scores having a lower interrater agreement than those of personality (Weiss et al. 2006). Also, while rater variance was small compared to genetic and environmental variance, as shown by the high interrater reliability estimates, raters contributed to some of the covariance among personality traits and between personality traits and subjective well-being. Rater covariance effects that go in the same direction as the animal effects would tend to inflate the magnitude of the observed correlations. Thus, we found that the phenotypic correlations as estimated by the genetic and environmental covariances between subjective well-being and Extraversion, Neuroticism, and Agreeableness were smaller than the observed correlations previously reported (Weiss et al. 2006), which were inflated by covariance introduced by the raters. The opposite was true for Dominance; the animal and rater covariances went in opposite directions and cancelled out, explaining why no correlation was found between Dominance and subjective well-being at the phenotypic level (Weiss et al. 2006).

Table 3 Heritability estimates for the combined sample and each species

	h^2			H^2		
	Combined	Bornean	Sumatran	Combined	Bornean	Sumatran
Extraversion	.23 (.13, .45)	.29 (.10, .55)	.22 (.09, .45)	.66 (.41, .86)	.67 (.43, .89)	.73 (.40, .87)
Dominance	.22 (.08, .42)	.26 (.08, .54)	.19 (.06, .46)	.78 (.49, .93)	.72 (.36, .91)	.78 (.43, .93)
Neuroticism	.22 (.12, .42)	.25 (.13, .53)	.29 (.14, .52)	.69 (.48, .85)	.68 (.40, .85)	.70 (.50, .87)
Agreeableness	.22 (.06, .38)	.25 (.09, .55)	.16 (.07, .43)	.82 (.41, .91)	.69 (.43, .90)	.71 (.40, .92)
Intellect	.29 (.14, .52)	.27 (.10, .53)	.28 (.15, .58)	.69 (.47, .86)	.64 (.38, .88)	.73 (.46, .89)
SWB	.24 (.07, .47)	.19 (.06, .60)	.23 (.06, .48)	.77 (.44, .92)	.72 (.32, .90)	.78 (.40, .92)

Posterior modes of narrow-sense, $h^2 = V_A/(V_A + V_D + V_E)$, and broad sense, $H^2 = (V_A + V_D)/(V_A + V_D + V_E)$, heritability with 95% credible intervals in parentheses

Table 4 Genetic, environmental, and rater correlations

	Extraversion	Dominance	Neuroticism	Agreeableness	Intellect
Additive genetic r_A					
Dominance	.14 (−.24, .37)				
Neuroticism	−.01 (−.24, .37)	−.04 (−.30, .33)			
Agreeableness	.17 (−.12, .52)	−.20 (−.49, .19)	−.03 (−.38, .28)		
Intellect	.08 (−.22, .39)	.17 (−.11, .50)	−.10 (−.42, .16)	.01 (−.38, .28)	
SWB	.23 (−.15, .45)	.13 (−.21, .43)	−.16 (−.47, .13)	.12 (−.19, .47)	.10 (−.18, .46)
Nonadditive (dominance) genetic r_D					
Dominance	.13 (−.20, .45)				
Neuroticism	−.03 (−.29, .30)	.034 (−.29, .31)			
Agreeableness	.29 (−.02, .55)	−.22 (−.55, .12)	−.13 (−.48, .13)		
Intellect	.15 (−.17, .40)	.20 (−.15, .47)	−.16 (−.47, .10)	.06 (−.23, .39)	
SWB	.22 (−.09, .51)	.14 (−.24, .44)	−.17 (−.48, .07)	.20 (−.07, .56)	.25 (−.11, .47)
Unique environment r_E					
Dominance	.16 (−.21, .44)				
Neuroticism	−.03 (−.30, .31)	−.02 (−.31, .30)			
Agreeableness	.31 (.02, .59)	−.21 (−.52, .14)	−.16 (−.48, .13)		
Intellect	.12 (−.12, .47)	.13 (−.18, .44)	−.15 (−.45, .11)	.16 (−.19, .46)	
SWB	.26 (−.07, .51)	.02 (−.30, .40)	−.25 (−.50, .04)	.30 (−.06, .54)	.20 (−.10, .50)
Rater r_j					
Dominance	.11 (−.15, .30)				
Neuroticism	−.10 (−.30, .19)	.36 (.12, .55)			
Agreeableness	.41 (.16, .57)	−.10 (−.40, .10)	−.21 (−.38, .10)		
Intellect	.20 (.06, .51)	−.17 (−.35, .13)	−.44 (−.54, −.09)	.30 (.04, .50)	
SWB	.24 (.00, .46)	−.17 (−.39, .13)	−.36 (−.55, −.09)	.30 (.06, .55)	.41 (.16, .61)

Parameter estimates shows in 95% credible intervals in parentheses
 SWB subjective well-being

Table 5 Scale consistency and reliability of assessments by multiple raters

	Consistency	Reliability
Extraversion	.28 (.24, .33)	.81 (.71, .87)
Dominance	.38 (.34, .44)	.87 (.81, .91)
Neuroticism	.23 (.20, .28)	.86 (.73, .90)
Agreeableness	.41 (.38, .48)	.77 (.64, .82)
Intellect	.31 (.25, .35)	.73 (.60, .83)
SWB	.49 (.42, .54)	.60 (.50, .74)

Parameter estimates with 95% credible intervals in parentheses. SWB subjective well-being. Domain-scale consistency calculated as $(V_{RPT} + V_J)/(V_{RPT} + V_J + V_R + 1)$; latent reliability calculated as $V_{RPT}/(V_{RPT} + V_J)$ where $V_{RPT} = V_A + V_D + V_E$

While our analysis models rater effects or perceptions that introduce correlations among the personality and subjective well-being dimensions, it does not address to what extent the five personality dimensions themselves are products of rater beliefs and perceptions. The generalizability of chimpanzee personality dimensions across samples living in different environments (King et al.

2005; Weiss et al. 2007) and raters with different cultural backgrounds (Weiss et al. 2009), their relationship with observed behaviors (Pederson et al. 2005), and the recoverability when rater effects on chimpanzee and orangutan personality structure have been removed (Weiss et al. 2012) indicate that the structure of these nonhuman primate personality dimensions is inconsistent with them being solely an artifact of human perception. Furthermore, although similar, the personality structure of orangutans is not identical to that of humans and the personality structure of humans, chimpanzees, and orangutans differ in ways consistent with phylogeny (e.g., humans and chimpanzees share a personality domain, Conscientiousness, that is absent in orangutans) and social structure (e.g., the primacy of the chimpanzee Dominance domain) (Weiss and Adams 2008). However, even factor models of human personality can be understood in terms of our faculties for social perception (Srivastava 2010) and thus rater-based assessments of nonhuman primate personality may miss individual differences that are entirely absent in humans (Uher 2008a, b). Understanding the full genetic structure of orangutan personality may

very well require multiple methods for measuring behavioral variation.

The quantitative genetic structure of personality within one species cannot act as strong evidence for past and current evolutionary scenarios (Gangestad 2011; Keller 2007). However, finding similar patterns of additive versus nonadditive genetic variation in human and orangutan personality suggests that similar processes of mutation and selection maintain variation in both species. A high proportion of nonadditive genetic variance is consistent with long-term selection on a trait (Crnokrak and Roff 1995; Merilä and Sheldon 1999) and while it may be a sign of strong selection reducing the additive genetic variance (Stirling et al. 2002) it is not indicative of recent selection (pace Figueredo and Rushton 2009; Penke et al. 2007). The recentness of novel selective pressures operating on human psychological characteristics since the agricultural revolution (~10 kya), which we interpret as the meaning of ‘recent’ in this context (see Figueredo et al. 2011), is a matter of perspective, as they are long-term compared to contemporary selection (Stearns et al. 2010) but recent relative to evolution before the split between human and chimpanzee lineages. Whether the large nonadditive genetic variance in orangutan and human personality evolved independently or is the result of long-term selection common in both species’ ancestor could be investigated by estimating dominance or epistatic genetic sources of variation in chimpanzees. While we did not have the power to explore species differences in genetic structure between Bornean and Sumatran orangutans, future studies of orangutans or other closely related species (such as in macaques) or subspecies (such as in chimpanzees) may be informative. Such studies may also lead to an understanding of the genetic underpinnings of species divergence in personality dimensions, such as whether the genetic correlation we found between Extraversion and Agreeableness is related to the blend, at the phenotypic level, of these two domains in rhesus macaques (Weiss et al. 2011b). Furthermore, the presence of nonadditive genetic variance in bird personality (van Oers et al. 2004) suggests that this phenomenon may be a more general part of how personality evolves.

This study highlights how studying personality and subjective well-being heritability in other primates is a useful approach to understanding the evolution of these traits in humans. In doing so these findings suggest that evolutionary psychologists interested in these problems need to reach back further than the Pleistocene and grapple with an evolutionary story that is at least 15 million years old, and probably older.

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